The Soft-plumaged Petrel, the Gon-gon and the Freira, Pterodroma mollis, P. feae and P. madeira

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The soft-plumaged petrels allied to *Pterodroma mollis* are a complex group of seabirds of wide distribution but uncertain affinities whose classification has caused repeated difficulty to systematists (Murphy & Mowbray 1951, Bourne 1957, 1966). In the past I have urged a cautious approach pending the acquisition of more information, a course adopted by Jouanin & Mougin (1979); but since the only important recent information indicates that a number of colonies may have been lost and the remainder include some of the rarest seabird populations in the North Atlantic (Bourne 1965, 1972, Bannerman 1965, 1968, Cramp & Simmons 1977), it seems time to reconsider their importance before we lose these as well. They are currently both the subject of debatable propositions about the difference between dark and light individuals of the same species (Clancey *et al.* 1981) and of intrinsic interest in their own right.

DISCOVERY AND DESCRIPTION

The first soft-plumaged petrel appears to have been collected at 6° 50′ N, 23° 46′ W off west Africa in October 1768 during Cook's first voyage. It was named *Procellaria crepidata* by D. C. Solander in his notes and this was the name used in some accounts of the voyage, though unfortunately no description was published at the time. An excellent drawing by Sydney Parkinson has since been reproduced by Lysaght (1959), from which it is recognisable as the form breeding locally in the Cape Verde Islands, where it is known as the Gon-gon, which was eventually named *Oestrelata feae* by Salvadori (1899). This still appears to be the only record of the collection of an example of the North Atlantic populations at sea, and confirms that this form has a primarily tropical distribution.

A number of specimens, including an almost uniformly dark grey bird, were next collected in the Southern Ocean by Gould (1860) on the way to Australia in 1838, and subsequently he obtained others from sailors. Gould (1844) published the first description of the main southern population under the name *Procellaria mollis*. He deduced that while the adults have white breasts, the young are grey (as in gulls), repeating this in his influential books on the birds of Australia. When it was eventually realised that while few petrels show much variation in appearance with age, many are polymorphic,

P. mollis was therefore assumed to be one of them.

Soon afterwards, in 1853, Frere obtained 2 more birds in Madeira (now at Cambridge—Benson in press). He presumably exhibited them as a new discovery, since shortly afterwards William Yarrell misidentified a stray specimen, without data, of the rather similar nominate race of Fairy Prion Pachyptila turtur as a new species from Madeira for Gould (1855) to describe and name Procellaria brevirostris. Fortunately this name had already been applied to the Kerguelen Petrel by Lesson (Bourne & Elliott 1965), so that while this mistake has caused a good deal of speculation, it has had no permanent nomenclatural consequences.

The situation was eventually investigated thoroughly by Mathews (1924, 1932, 1934 a). First he appropriately named another stray specimen of doubtful origin, now in the American Museum of Natural History (AMNH) as Pterodroma dubius, and what appears to be Gould's original grey "immature" in the British Museum (Natural History) (BMNH) as P. deceptornis. He followed this by describing a small population nesting in the mountains of Madeira, where they are known as the Freira, and large birds nesting on the offshore islands, as 2 new races, P.m. madeira and P.m. deserta. Finally in his definitive check-list (1934b) he synonymised all the southern birds under nominate P. mollis but continued to accept 3 races from the North Atlantic, including large P.m. feae from the Cape Verde Islands, P. m. deserta and P. m. madeira. Most subsequent authors have considered P. m. deserta inseparable from P. m. feae (Bourne 1957, Jouanin et al. 1969, Cramp & Simmons 1977).

Up to this time, apparently, it was assumed that the Soft-plumaged Petrels were most closely related to the larger members of the genus Pterodroma in the Southern Ocean. Then Murphy & Mowbray (1951) reported the rediscovery of the long-lost Bermuda Petrel P. cahow which proved to be intermediate in size and appearance between P. mollis and a group of large warmwater species including the Capped Petrel P. hasitata of the West Indies and the Dark-rumped and White-necked Petrels P. phaeopygia and P. externa of the Pacific (Bourne in Palmer 1962). I have already suggested that the full elucidation of the situation must depend on further investigation in the field, notably at another possible intermediate station, namely the Azores (Bourne

OBSERVATIONS IN THE FIELD

The appearance and behaviour of live Soft-plumaged Petrels has been examined critically by Elliott (1954, 1957) in the Tristan/Gough group. He found that while most had white breasts, one distinct group nesting high on the main island were darker with more markings below, though otherwise quite similar, and concluded therefore that they were only a variety. Simultaneously Rand (1954) reported what he took to be a uniformly dark form of P. mollis breeding commonly on Marion Island; so that the 2 authors, prior to publication, were consequently unable to to compare their observations. This was unfortunate, since the specimens that Rand sent to the

BMNH are in fact young Kerguelen Petrels (Bourne 1957).

In the course of an investigation of the birds of the North Atlantic islands I examined nearly all soft-plumaged petrel specimens in northern museums (Bourne 1957, 1966). They showed little consistent geographical variation except that while North Atlantic birds are usually pale and white below, the southern ones are darker with a breast-band. The birds from the North Atlantic are also divisible into 2 groups of different sizes with different breeding-seasons. Thus the small, form madeira lacks' much mottling and appears to breed in the early summer in the mountains of that island; and the large form feae, which tends to be streaked on the flanks, breeds in the autumn on the offshore islands of Madeira and in winter in the mountains of the Cape Verde Islands. About one in ten of all large series were darker and more heavily marked below and one in many hundreds of the southern population were dark all over.

Further summer-breeding populations of P. mollis which appear indistinguishable from the nominate form have also been found in the Southern Ocean at the Crozets by Despin et al. (1972) and on Antipodes Island, south of New Zealand, by Warham & Bell (1979). There is also a specimen of P. mollis in the BMNH collected in the 1840s by Ross' Antarctic Expedition and 2 others in the Melbourne Museum collected in February 1952 at Port Jeanne d'Arc from Kerguelen, from where Derenne et al. (1974) give other records. Individuals have also recently been reported from Macquarie and Chatham Islands (Jones 1980, Crockett 1981), where it now seems likely that bones formerly attributed on grounds of probability to the osteologically similar Mottled Petrel Pterodroma inexpectata, together with other bones from Amsterdam Island (Jouanin & Paulian 1960), really belong to further southern populations of P. mollis. While some of these populations may have been exterminated by introduced predators, it might still be worth searching for survivors (Bourne 1965, 1967, 1972, 1981).

Further observations have now confirmed that while heavily-marked individuals can normally be found in variable proportions in most or all populations of Soft-plumaged Petrel, and may apparently predominate in the Prince Edward Islands (Clancey et al. 1981), uniformly dark individuals are rare. In addition to the bird obtained in the last century by Gould (1844, see Mathews 1932), about 12 have now been reported at sea (Sinclair 1978) and on Gough Island (Swales 1965) in the Southern Ocean, while on Marion Island one was found consorting in a hole with a white-breasted individual (Schramm 1982). At sea the paler birds showed contrasting darker markings of the type usual in Soft-plumaged Petrels, while the darker birds were darker than Kerguelen Petrels, with which they might have been confused, and which appear silvery at sea. Sinclair (1978) reports also that P. mollis can be separated by its characteristic shape and behaviour and the darker leading edge of the underwing.

DISCUSSION

Any attempt to classify the Soft-plumaged Petrels and their allies encounters difficulties resulting from either gaps or overlaps in their distribution, suggesting that either the missing populations are likely to have been lost or overlooked, as in the subantarctic islands of New Zealand or the Azores; or that the overlapping populations must either interbreed or represent separate species (Mayr et al. 1953: 121). It may be useful to consider the problem under 3 headings.

The medium-sized gadfly (or Soft-plumaged) petrels of the Southern Ocean

Owing to the fact that the most important early authority, Gould (1844, 1860), apparently collected only one medium-sized grey gadfly petrel in the Southern Ocean, which by chance proved to be the rare dark form of *P. mollis*, there appears to have been persistent confusion over the relationship of this species to the more southerly grey Kerguelen Petrel *P. brevirostris* (Falla 1937, Rand 1954). Until I saw them together I also assumed that they must be closely related and might hybridise (Bourne 1966). In fact they appear to be rather distinct with numerous isolating mechanisms.

Thus, in the first place, while the Soft-plumaged and Kerguelen petrels are rather similar in size and sometimes in appearance, they differ considerably in their structure and behaviour, the Kerguelen Petrel having a much larger eye, presumably an adaption for nocturnal vision in particular (Harper 1973). Secondly, they also have rather distinct annual cycles, the Kerguelen Petrel laying about 2 months earlier in the spring and completing its breeding

cycle rapidly during the summer (Mougin 1969); the Soft-plumaged Petrel in contrast continues to feed its chick into the winter. Thirdly, I found that on Gough Island the 2 species use rather different nest-sites, the subtropical Soft-plumaged Petrels breeding in dry, sheltered burrows in the steep sides of the island, while the subantarctic Kerguelen Petrels preferred waterlogged

holes in the bleak upland heaths.

Similarly, while I formerly supposed that both species were originally replaced by the rather similar Mottled Petrel P. inexpectata in the New Zealand area until the sites were devastated by introduced predators (Bourne 1957), the presence of P. inexpectata on the outlying islands has never been proved, while P. mollis has in fact been found there instead. It consequently seems more likely that P. inexpectata was a specialised form which developed on and around the main islands of New Zealand, dispersing south in the summer and migrating into the northern hemisphere in the winter, whereas the sedentary P. mollis continued to occupy the same niche on the outlying islands that it does in the Atlantic and Indian Oceans. (Incidentally I have seen P. mollis commonly at sea much further east in the Great Australian Bight than shown on the distribution map in Harper (1973).)

The medium-sized gadfly petrels of the North Atlantic

While the Soft-plumaged Petrels of the Southern Ocean may vary in their appearance, they are all rather similar in their size and habits, nesting on the middle slopes of oceanic islands in the local summer. The situation is rather different in the North Atlantic, where, as already mentioned, in addition to a population of small-sized birds nesting in the summer on the cool, moist, heavily-vegetated upper slopes of Madeira, other groups of larger-sized birds breed in the autumn on its bare, arid outlying islands, and in the winter on the mountains of the Cape Verde Islands to the south and islets around Bermuda to the west.

This situation is susceptible to 2 alternative explanations. All the birds may possibly be derived (together with *P. cahow* of Bermuda) from the large, winter-nesting Capped Petrel *P. hasitata* of the West Indies. This could have given rise when the climate deteriorated during the Pleistocene to a summernesting population on the mountains of Madeira, which subsequently colonised the Southern Ocean, where it is now replacing *P. inexpectata* in the New Zealand area following reduction of the latter by introduced predators. Alternatively the eastern North Atlantic populations may be derived from summer-nesting birds of the Southern Ocean, which colonised the North Atlantic during the Pleistocene, and since the climate became warmer have given rise to a winter-nesting population in the Cape Verde Islands, and have now colonised the lower levels of the Madeira group as well.

The relationship between birds of different colours

On the basis of a personal examination of specimens in northern collections, including all the types, it is clear (see above) that while northern populations of the Soft-plumaged Petrels are normally pale with white breasts, and the southern ones darker with a band across the breast, occasional individuals in all populations are darker with more marking below, or even dark all over in the southern populations. The examination of many more specimens including recent series from the Antipodes and Crozet islands confirms this.

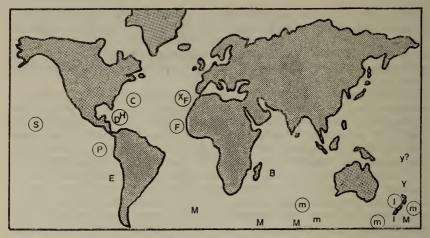


Figure 1. Breeding distribution of Soft-plumaged and Capped Petrels.

M-Soft-plumaged Petrel Pterodroma mollis. I-Petrel Mottled Petrel P. inexpectata.
F-Gon-gon P. feae. X-Freira P. madeira. C-Bermuda Petrel P. cahow. H-Capped Petrel P. hasitata. D-Jamaica Petrel P.h. caribbaea. P-Dark-rumped Petrel P. phaeopygia. S-Hawaiian Petrel P.p. sandwichensis. E-Juan Fernandez Petrel P. externa. Y-White-necked Petrel P. e. cervicalis. B-Barau's Petrel P. baraui. Populations circled are already known to be severely reduced in numbers, and those with small letters are only known from stray specimens and bones; the Jamaica Petrel (D) may be extinct.

Clancey et al. (1981) have recently deduced instead, from South African specimens from a more limited series of sites, that the darker birds belong to a distinct race, P. m. dubia Mathews (1924), breeding in the southern Indian Ocean and expected to occur on Antipodes Island in the South Pacific. Regrettably, in fact, the type of P. m. dubia is so worn that it is difficult to be sure of its original appearance in the absence of information about its origin. Clancey et al. also report the occurrence of two small, pale petrel corpses resembling the North Atlantic race P. m. madeira on South African beaches.

In addition to the dark birds collected on Tristan by Elliott (1954), the BMNH also contains 2 small, pale birds, possibly immatures, which Elliott collected on nearby Inaccessible Island in May 1952. There is also a third, in spirit, collected on Marion Island in March 1961. Thus the full range of variation in the southern populations has now been collected in both the Tristan/Gough and Prince Edward groups and, as reported by Warham & Bell (1979), the Antipodes birds show a similar variation in appearance.

It appears that while the soft-plumaged petrels allied to *P. mollis* become darker and more heavily marked from north to south, there is a wide range of variation and overlap in their appearance, so that plumage is not a very satisfactory basis for their classification. The populations in the Southern Ocean, which all appear to nest in the summer, are otherwise rather uniform in such characters as size and behaviour, and seem rather distinct from other southern petrels except possibly *P. inexpectata*, which differs in its voice (Warham 1979) and migratory habits; thus there seems little case for recognising racial variation there. The North Atlantic populations are more

variable in size and annual cycle, intergrading through madeira, feae and cahow with the large, winter-nesting Capped Petrel P. hasitata of the West

Indies (Fig. 1).

While there is at present an important gap in the North Atlantic range of the group in the inadequately-explored Azores, where the birds may either have been overlooked or exterminated by introduced predators, Madeira appears to have been colonised twice. Presumably it was first occupied by the small, summer-nesting Freira madeira when it was cooler and wetter during the Pleistocene; but madeira has now become restricted to the upper slopes and the low ground has been colonised by the larger, winter-nesting Gon-gon feae, derived from the same stock but under the more arid conditions of the Cape Verde Islands since the climate became warmer in recent times. In consequence the Madeira area, which appears to have the best conditions for subtropical petrels in the North Atlantic, is now exploited by birds of a wider range of sizes breeding during much of the year.

The most important conclusion arising from recent observations, for which I am indebted to C. Jouanin, R. de Naurois, G. Le Grand and D. Wingate, is that all the North Atlantic *Pterodroma* petrels are now rare and threatened, with *cahow* and *madeira* in particular already reduced to a few dozen birds. In this situation there has been a strange contrast between the assistance given to the Cahow, which has been regarded as a species and has received world-wide attention and special assistance (so that it is now recovering), and the Freira, which has been well-nigh ignored as a dubious race. The Gon-gon and the Freira are in fact sympatric forms of great interest which are both in grave danger on Madeira. Because it is difficult to say which of the two is closer to the Soft-plumaged Petrel, showing as the latter does an overlap in its variation in colour, it seems time to abandon taxonomic caution and I advocate treating all 3 binomially as distinct species, *Pterodroma mollis*, *Pterodroma feae* and *Pterodroma madeira*.

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